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Allometric prediction of above-ground biomass of eleven woody tree species in the Sudanian savanna-woodland of West Africa

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Abstract: Allometric models are necessary for estimating biomass in terrestrial ecosystems. Generalized allometric relationship exists for many tropical trees, but species- and region-specific models are often lacking. We developed species-specific allometric models to predict aboveground biomass for 11 native tree species of the Sudanian savanna-woodlands. Diameters at the base and at breast height, with species means ranging respectively from 11 to 28 cm and 9 to 19 cm, and the height of the trees were used as predictor variables. Sampled trees spanned a wide range of sizes including the largest sizes these species can reach. As a response variable, the biomass of the trees was obtained through destructive sampling of 4 754 trees during wood harvesting. We used a stepwise multiple regression analysis with backward elimination procedure to develop models separately predicting, total biomass of the trees, stem biomass, and biomass of branches and twigs. All species-specific regression models relating biomass with measured tree dimensions were highly significant ($p < 0.001$). The biomass of branches and twigs was less predictable compared to stem biomass and total biomass, although their models required fewer predictors and predictor interactions. The best-fit equations for total above-ground biomass and stem biomass had $R^2 > 0.70$, except for the *Acacia* species; for branches including twig biomass, R^2-values varied from 0.749 for *Anogeissus leiocarpa* to 0.183 for *Acacia macrostachya*. The use of these equations in estimating available biomass will avoid destructive sampling, and aid in planning for sustainable use of these species.

Keywords: allometry; above-ground biomass; indigenous woody species; linear regression; site specific equation

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Introduction

Accurate estimates of aboveground woody biomass of tropical trees are essential for a host of reasons. Estimating above-ground tree biomass and biomass components are essential for assessing structural and functional attributes of forest ecosystems across a wide range of environmental conditions (Chave et al. 2005) and can be used as an indicator of site productivity, both biological and economic (Navar 2009a), particularly in tropical countries where forests are undergoing the highest rates of change. Estimates of the biomass can aid the quantification of forest resources such as availability of woodfuel and timber. In addition, estimates of above-ground biomass are essential for studies of carbon stocks and the effects of deforestation and carbon sequestration on the global carbon balance (Brown et al. 1989; Litton and Kauffman 2008). It also provides valuable information for understanding the role of energy and nutrient flows. Estimates of the potential of these sinks and sources of carbon require reliable estimates of the biomass as a basis. Yet, accurate estimates in many tropical regions are lacking, due to difficulties in obtaining field data for establishing appropriate allometric models for

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predicting biomass of individual trees in species-rich ecosystems (Chave et al. 2005).

Biomass can be estimated by direct or indirect methods. Direct measurement of tree biomass involves felling an appropriate number of trees and estimating their field- and oven-dry weights, a method that can be costly and impractical, especially when dealing with numerous species and large sample areas (Willebrand et al. 1993). Rather than always performing destructive sampling in the field, an alternative method is to use allometric regression equations that predict the biomass component given some easily measurable predictor variables, such as trunk diameter, shoot height or crown diameter, which can be measured non-destructively (Whittaker 1968). Baskerville (1965) has shown that the most accurate method is to calculate regression equations from destructively sampled trees in the size range of interest and apply them to every tree in the stand.

Different types of regression equations (linear, logarithmic, exponential and power) are used to estimate biomass indirectly. Several generalized biomass prediction equations have been developed for tropical species (Stromgaard 1985; Brown et al. 1989; Overman et al. 1994; Chave et al. 2005; Cole and Ewel 2006), temperate species (Ter-Mikaelian and Korzukhin 1997) and world-wide species (Zianis and Mencuccini 2004) on the basis of the easily measured attributes of trees. The use of these equations for consistent forest biomass estimation for all species is however troublesome because there are many gaps among species, tree sizes, and geographic areas not covered by the equations (Navar 2009b). Furthermore, developers of these equations often caution against extrapolation beyond their study area (Grundy 1995; Navar 2002; Chave et al. 2005). Many factors can influence the accuracy of biomass estimations and are known to vary with environmental factors (e.g. soil type, soil nutrients, climate, disturbance regime, successional status, and topographic position), wood specific density, and genetic variation. Therefore biomass equations tailored to estimate biomass of a particular species in a given biome can provide more accurate estimates (Cole and Ewel 2006; Litton and Kauffman 2008) than generalized biomass equations.

In West Africa, harvesting of forests is essential for rural livelihoods as it provides employment, income as well as consumption goods and services. Firewood is the major source of energy used for cooking, heating and other domestic purposes, and woodfuel including fuelwood and charcoal accounts for about 90% of the total energy consumption (Brocard et al. 1998). The main vegetation cover used by the households to produce woodfuel is obtained from native forests. The overcutting of forests for fuel needs is exacerbated in drier and densely populated areas, resulting in rapidly shrinking forest cover and ecological imbalance. The sustainability of this high dependence is questionable and, increasingly, sound decisions by policy-makers regarding the management and use of forest and trees require better understanding of the carrying capacity of this biome for several purposes, including grazing, fuelwood, timber, other non-timber forest products, and environmental services provided by carbon sequestration. To meet these needs, reliable estimates on tree biomass are needed.

This study on ecology and productivity of fuelwood in the Sudanian savanna-woodlands was performed in conjunction with government regulated selective cutting management in two State forests. Species-specific allometric models to predict coarse woody biomass of stem, branches and twigs, and total above-ground biomass from dendrometric measurements of harvested trees, were developed for a group of species that have wide ecological distribution in West Africa. The purpose is to contribute to the understanding of woody biomass both from an ecological perspective and from the perspective of sustainable natural resource management.

Materials and methods

Study area

The experimental sites are located on flat areas in Laba (11°40' N, 2°50' W) and Tiogo (12°13' N, 2°42' W) State forests (forêts classées), both at an altitude of 300 m a.s.l in Burkina Faso, West Africa. The Laba and Tiogo State forests were delimited by the colonial French administration in 1936 and 1940 and cover 17 000 ha and 30 000 ha, respectively. Both forests are located along the only permanent river (Mouhoun, formerly known as Black Volta) in the country. The unimodal rainy season lasts for about six months, from May to October. Based on data collected from in situ mini-weather stations at each site, the mean annual rainfall for the period 1992–2008 was 886 ± 151 mm for Laba and 845 ± 168 mm for Tiogo, and the number of rainy days per annum was 69 ± 16 for Laba and 65 ± 11 for Tiogo. Mean daily minimum and maximum temperatures ranged from 16°C to 32°C in January (the coldest month) and from 26°C to 40°C in April (the hottest month). Most frequently encountered soils are Lixisols, and the soil at Laba is shallow (< 45 cm depth) silty-sand while it is mainly deep (> 75 cm) silty-clay at Tiogo. These soils are representative of large tracts of the Sudanian Zone in Burkina Faso. Phyto-geographically, the study sites are situated in the Sudanian regional centre of endemism in the transition from the north to south Sudanian Zone. The vegetation is characterized as a tree/bush savanna with the herbaceous layer dominated by perennial grasses, annual grasses and forbs. Trees and shrubs are dominated by the families of Mimosaceae and Combretaceae at both sites. In terms of basal area, the main woody species are *Detarium microcarpum* Guill. & Perr.*, Combretum nigricans* Lepr. ex Guill. & Perr.*, Acacia macrostachya* Reichenb. ex Benth.*, Entada africana* Guill. & Perr., *Anogeissus leiocarpa* (DC.) Guill. & Perr. and *Vitellaria paradoxa* C.F. Gaertn. Trees are mainly cut for commercial fuelwood and poles by local populations that are organised in cooperatives in both forests. The wood is transported to towns 50 km and 145 km away. The diameter of the trees cut range from 10 to 25 cm at breast height. In practice only the stems are transported to town for sale as woodfuel or construction wood. Branches are used locally for fuelwood. The twigs are often left on the ground to improve soil fertility and porosity, but can also be used as fuelwood.

Species

Eleven species belonging to three families- Combretaceae (*Anogeissus leiocarpa, Combretum ghasalense, C. glutinosum, C. micranthum, C. nigricans*), Leguminosae (*Acacia dudgeoni, A. macrostachya, Detarium microcarpum, Entada africana, Piliostigma thonningii*) and Rubiaceae (*Crossopterix febrifuga*) were selected for this study which is part of a larger long-term research project. All species sampled are native to the studied forests, have a diversity of ecological attributes and they are all species of socio-economic importance. Sampled trees spanned a wide range of sizes including the largest sizes these species can reach. All the species studied have wide distributions across the dry forests of the Sudanian zone (Arbonnier 2004), and they frequently account for most of the individuals and most of the biomass in areas dominated by native species.

Samples

The present study is part of a large factorial experiment with four replicates of 4.5 ha each established to study the long-term effects of grazing, prescribed fire and selective tree cutting on the ecology and productivity of the Sudanian savanna-woodlands (Savadogo et al. 2008). Intensive measurement during the selective cutting allowed us to develop allometric equations. The selective cutting was undertaken during the cool dry season (December 1993 at Tiogo and a month later in January 1994 at Laba) by removing 50% of the merchantable standing volume of the selected species. We attempted to harvest trees of deciduous species when they had shed their leaves since this period coincides with the stunting of the plant, and volume increment and biomass are constant (Bellefontaine et al. 2000; Smektala et al. 2002).

Prior to cutting, all species were categorized according to their local uses as: protected species, timber, poles, fuelwood and other uses. Individuals of all categories not considered as protected species were cut. Girth at 20 cm (Db) and 130 cm (Dbh) along the stem as well as stem height (H) were measured on all stems having a girth ≥10 cm (limit applied at 20 cm and 130 cm) over bark. For trees forking below 130 m, the circumferences of all ramifications were measured and later the equivalent diameter was calculated as: $DBH = \left(\sum_{i=1}^{n} DBH_i^2 \right)^{1/2}$. Total stem length was measured for all stems including those that did not reach the 10 cm girth limit using height-measuring pole (for stem ≤ 6 m) or a clinometer (for stem ≥ 6m). In total, 4 754 trees were harvested. The dimensions of these trees are summarized in Table 1. The mean diameter at the base of each species harvested surpassed 11 cm and the largest value was 28.17 ± 1.33 cm for *A. leiocarpa*; the total height varied from 3.6 to 7.8 m. In terms of Dbh and height, *A. leiocarpa* was the largest species followed by *C. febrifuga*. More than half of the studied species had their average Dbh less than 10 cm.

Harvested trees were cut into their component parts. The trees were debranched to obtain a clear stem and then cut into sections to facilitate weighing in the field. Wood discs were taken from the base, middle and top of the stem (i.e. at 0, 50%, and 100% of stem total length) and were subsequently weighed. The component parts were then sub-sampled for moisture determination. Representative samples of branches and twigs were also obtained and weighed. The wood discs (2 cm thick) and the samples of branches and twigs (15 cm in length) were air-dried until constant weight. Dry to fresh weight ratios were developed for each sample of each component and multiplied by the fresh weight of the biomass component to calculate dry biomass. The mean total above-ground dry biomass per harvested individual of the studied species ranged from 361.46 ± 47.80 kg for *A. leiocarpa* to 26.45 ± 0.86 for *A. macrostachya*. Stem wood constituted more than two thirds of the total standing woody biomass for each individual tree (Table 1). The allometric equations were developed using Db (diameter at stump level), Dbh (diameter at breast height) and height (H) data vs. component biomass through regression models.

Statistical analysis

We used a stepwise multiple regression analysis with backward elimination procedure to develop models predicting the total biomass of the tree and its constituent biomass separately i.e., the stem biomass in one hand, and branches and twigs, on the other. All dendrometric parameters; diameter at stump level in cm (Db), diameter at breast height in cm (Dbh) and height of the tree in cm (H) were used as predictor variables to compensate for the less consistent architecture and complicated branching patterns of trees in dry forest ecosystems that often make biomass prediction problematic (Cole and Ewel 2006).

For each species and each woody biomass component, the most complicated model, including interactions between all explanatory variables was first fitted. Subsequently, models were continuously updated taking away non-significant terms until a minimal model was reached with all terms being significant. In cases where some interaction terms were significant while the main effects were not, the non significant main effect terms were kept in the model (Crawley 2005; Zuur et al. 2009). To visualize the predictability of the models, the predicted values from each model were plotted against the observed values. Log transformed response variable was used in the model-fitting as it substantially improved the homoscedasticity and the normality of the data, and in general, the fit of the model. For species such as *D. microcarpum* and *E. africana,* however, the distribution of the residuals deviated from normality which is difficult to reach with large data sets. It is also known that large data sets mitigate the effect of deviation from normality (Faraway 2005). The assumption of multicolinearity was considered as not violated since none of the explanatory variable showed a correlation coefficient of at least 0.9 with another variable (Tabachnick and Fidell 1996). In general, tree individuals with values that appeared to be typesetting error (unreliably large values and very small values which could not be expected from their dendrometric measurements) and suggested by the model assumptions checking as outliers (residuals vs. leverage plot), were removed. All analyses were

performed using the R statistical package (R Development Core Team 2009).

Table 1. Sample size, range of dendrometric variables and dry weight biomass component of stem, branches + twigs and total above-ground biomass for the sample trees. Values are mean ± standard error
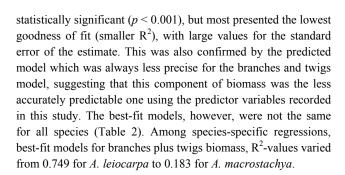
Species	Number of the trees harvested	Diameter at stump level (D base, cm)	Diameter at breast height (DBH, cm)	Height (cm)	Total Biomass (kg)	Stems (kg)	Branches (kg)
A. dudgeoni	558	11.828 ± 0.135	8.987 ± 0.123	464.229 ± 4.607	41.155 ± 1.316	30.541 ± 1.041	10.614 ± 0.338
A. macrostachya	523	11.090 ± 0.148	7.206 ± 0.110	391.205 ± 3.773	26.447 ± 0.862	19.283 ± 0.659	7.164 ± 0.330
A. leiocarpa	120	28.173 ± 1.334	19.752 ± 1.173	782.50 ± 21.603	361.464 ± 47.797	320.953 ± 44.748	40.511 ± 3.705
C. ghasalense	433	14.060 ± 0.275	8.975 ± 0.196	385.381 ± 5.156	49.405 ± 2.611	36.304 ± 2.105	13.101 ± 0.616
C. glutinosum	103	14.285 ± 0.629	9.594 ± 0.392	476.019 ± 14.179	50.920 ± 6.262	42.262 ± 5.539	8.658 ± 0.954
C. micranthum	89	11.832 ± 0.545	7.490 ± 0.379	451.011 ± 11.499	28.841 ± 3.537	21.476 ± 2.756	7.365 ± 0.852
C. nigricans	98	17.509 ± 0.694	11.407 ± 0.431	530.306 ± 15.804	84.796 ± 8.640	71.317 ± 7.557	13.479 ± 1.283
C. febrifuga	253	21.806 ± 0.451	15.293 ± 0.355	570.119 ± 9.404	110.374 ± 5.837	93.462 ± 5.234	16.912 ± 0.870
D. microcarpum	1177	18.044 ± 0.130	12.731 ± 0.105	526.321 ± 3.523	73.003 ± 1.638	61.749 ± 1.460	11.254 ± 0.285
E. africana	957	13.820 ± 0.141	9.920 ± 0.123	490.982 ± 4.748	37.912 ± 1.182	32.160 ± 1.059	5.753 ± 0.221
P. thonningii	443	13.178 ± 0.212	9.303 ± 0.167	363.061 ± 4.041	36.071 ± 1.654	29.427 ± 1.426	6.644 ± 0.394

Results

All species-specific regression models relating biomass with measured tree dimensions were highly significant ($p < 0.001$). The goodness of fit for the total dry weight biomass was the highest for *A. leiocarpa* ($R^2 = 0.905$) followed by *C. nigricans* ($R^2 = 0.900$). In general, except for the two *Acacia* species, the total biomass production was quite predictable (R^2 adjusted ≥ 0.7) and all models allow reasonably good estimates of the biomass production of the studied species from their dendrometric measurements (Table 2). The number of predictor parameters and parameter interactions required by the equations was different for different species. The simplest model (two main effects and only one first order interaction term) was obtained for the species *C. glutinosum* and it also had high predictability ($R^2 = 0.852$). Five other species had simple models (main effects and only one interaction term). *A. macrostachya* had the most complicated model (with all interaction terms) and also with less prediction power ($R^2 = 0.428$).

The allometric equations for the dry weight of stems generally fit the data well, and in most cases except the two *Acacia* species, the magnitude of the relationship was more than 70%. The observed variation in biomass was explained by diameters (Db and Dbh), height and some interaction factors. All equations were highly significant ($p < 0.001$). For *D. microcarpum*, *C. febrifuga*, *P. thonningii*, *A. dudgeoni* and *A. macrostachya*, the fit of the relationship was slightly stronger with stem dry weight compared to total biomass. In the case of all the other species it was the opposite. The best fits of this biomass component were obtained in decreasing order for *C. nigricans*, *A. leiocarpus* and *C. glutinosum* which all had $R^2 > 0.8$.

In general, biomass of branches and twigs was less predictable compared to stem biomass and total biomass, although their models required fewer predictors and predictor interactions (Table 2). All the species-specific regression equations relating branches and twig biomass with measured plant dimensions were

statistically significant ($p < 0.001$), but most presented the lowest goodness of fit (smaller R^2), with large values for the standard error of the estimate. This was also confirmed by the predicted model which was always less precise for the branches and twigs model, suggesting that this component of biomass was the less accurately predictable one using the predictor variables recorded in this study. The best-fit models, however, were not the same for all species (Table 2). Among species-specific regressions, best-fit models for branches plus twigs biomass, R^2-values varied from 0.749 for *A. leiocarpa* to 0.183 for *A. macrostachya*.

Discussion

A systematic screening of the regression models for estimating above-ground biomass and tree components showed that tree diameter (Db and Dbh), tree height and combination of these variables could be used as predictor variables. The allometric equations were relatively satisfactory for predicting total above-ground biomass and the total variation explained by the relationships was above 50% except for *A. macrostachya*. Actual model performance, expressed as goodness of fit (R^2) depended on both the species involved and the biomass component to be estimated. The relationship was much stronger for trees with larger biomass weights (i.e., those having a larger proportion of their biomass in the stem or total aboveground biomass such as *A. leiocarpa, C. nigricans* and *C. febrifuga*). Allometric relationships being different for different tree species have been reported previously and mainly attributed to differences in the specific gravity (weight per volume) of the species' wood (Komiyama et al. 2002; Aboal et al. 2005; Navar 2009b). In general, there is a variability of basic density among individuals of a given species, among geographical locations and with age (Wiemann and Williamson 1989; Fearnside 1997; Nygard and Elfving 2000). Moreover, wood specific gravity of most of the species from the study sites differs among the tree sections: it is higher at breast height than at the top of bole and also higher at the base of the tree stem than that at the base of the living crown (Nygard and Elfving 2000)

which could explain the fact that total biomass of the studied species was mainly concentrated in the stems.

Table 2. Relationship between tree dendrometric variables: height (H), diameter at base (Db) and diameter at breast height (Dbh), and dry weight biomass components of stem (Ws), branches + twigs (Wb) and total above ground dry biomass (Wt) of 11 Sudanian savanna woody species (Log transformed response variable Wt, Ws and Wb were used).

Tree species	Total above ground dry biomass (Wt)	Dry weight biomass components of stem (Ws)	Branches + twigs (Wb)
Acacia dudg-eoni	Wt=0.938+0.119Db+0.099Dbh+0.001H-0.004Db×Dbh R^2=0.569 Res.df=553 F=184.5 p<0.001 SEE=0.435	Ws=0.604+0.116Db+0.1Dbh+0.001H-0.003Db×Dbh R^2=0.576 Res.df=553 F=190.2 p<0.001 SEE=0.453	Wb=0.077+0.171Db+0.027Dbh-0.0001H-0.009Db×Dbh+0.0002Dbh×H R^2=0.340 Res.df=552 F=58.34 p<0.001 SEE=0.585
Acacia mac-rostachya	Wt=3.935-0.199Db-0.088Dbh-0.007H+0.017Db × Dbh + 0.0008Db × H +0.006Dbh×H-0.00006Db×Dbh×H R^2=0.428 Res.df=515 F=56.82 p<0.001 SEE=0.516	Ws=2.970-0.137Db-0.082Dbh-0.006H+0.015Db×Dbh +0.0007Db×H-0.00006Db×Dbh×H R^2=0.473 Res.df=515 F=67.79 p<0.001 SEE=0.524	Wb=0.211+0.044Db+0.071Dbh+0.001H R^2=0.183 Res.df=519 F=39.84 p<0.001 SEE=0.752
Anogeissus leiocarpa	Wt=-0.889+0.107Dbh+0.304Dbh+0.004H-0.006Db×Dbh-0.00002Db×H-0.0002Dbh×H+0.000004Db×Dbh×H R^2=0.905 Res.df=112 F=162.8 p<0.001 SEE=0.401	Ws=-0.876+0.085Db+0.329Dbh+0.003H-0.007Db×Dbh +0.00001Db×H-0.0002Db×H+0.000005Db×Dbh×H R^2=0.878 Res.df=112 F=123 p<0.001 SEE=0.483	Wb=-2.736+0.134Db+0.184Dbh+0.006H-0.003Db×Dbh-0.0001Db×H-0.0002Dbh×H+0.000003Db×Dbh×H R^2=0.749 Res.df=112 F=51.61 p<0.001 SEE=0.564
Combretum ghasalense	Wt=-0.961+0.086Db+0.168Dbh+0.0009H-0.004Db×Dbh R^2=0.708 Res.df=428 F=263.2 p<0.001 SEE=0.471	Ws=0.508+0.086Db+0.169Dbh+0.001H-0.003Db×Dbh R^2=0.726 Res.df=428 F=286.4 p<0.001 SEE=0.476	Wb=-0.056+0.095Db+0.178Dbh-0.005Db×Dbh R^2=0.514 Res.df=429 F=153.2 p<0.001 SEE=0.611
Combretum glutinosum	Wt=0.661+0.121Db+0.190Dbh-0.005Db×Dbh R^2=0.852 Res.df=99 F=196.1 p<0.001 SEE=0.349	Ws=0.470+0.104Db+0.198Dbh-0.004Db×Dbh R^2=0.848 Res.df=99 F=191.1 p<0.001 SEE=0.368	Wb=-0.617+0.152Db+0.219Dbh-0.002H-0.007Db×Dbh R^2=0.601 Res.df=98 F=39.38 p<0.001 SEE=0.573
Combretum micrantum	Wt=0.827+0.184Db+0.037Dbh-0.001Db×Dbh+0.0004Dbh×H R^2=0.671 Res.df=83 F=36.89 p<0.001 SEE=0.473	Ws=0.646+0.177Db+0.026Dbh-0.002Db×Dbh+0.0004Dbh×H R^2=0.691 Res.df=83 F=40.39 p<0.001 SEE=0.469	Wb=-0.900+0.196Db+0.136Dbh-0.008Db×Dbh R^2=0.44 Res.df=85 F=24.04 p<0.001 SEE=0.656
Combretum nigricans	Wt=0.213+0.132Db+0.204Dbh-0.0007H-0.005Db×Dbh R^2=0.900 Res.df=93 F=218.7 p<0.001 SEE=0.318	Ws=-0.531+0.168Db+0.090Dbh+0.004H-0.0002Db×H R^2=0.897 Res.df=93 F=213.1 p<0.001 SEE=0.336	Wb=-1.164+0.031Db+0.236Dbh+0.003H-0.0002Dbh×H R^2=0.670 Res.df=93 F=50.27 p<0.001 SEE=0.563
Crossopterix febrifuga	Wt=0.933+0.030Db+0.178Dbh+0.002H-0.002Db×Dbh+0.00007Db×H-0.0001Dbh×H R^2=0.800 Res.df=246 F=168.7 p<0.001 SEE=0.360	Ws=0.625+0.035Db+0.176Dbh+0.002H-0.002Db×Dbh+0.00007Db×H-0.00009Dbh×H R^2=0.809 Res.df=246 F=178.9 p<0.001 SEE=0.363	Wb=-0.456+0.155Dbh+0.003H-0.0001Dbh×H R^2=0.475 Res.df=249 F=76.9 p<0.001 SEE=0.597
Detarium microcarpum	Wt=0.758+0.028Db+0.237Dbh+0.0009H-0.003Dbh+0.0001Db×H-0.0002Dbh×H R^2=0.731 Res.df=1170 F=532.8 p<0.001 SEE=0.352	Ws=0.473+0.029Db+0.242Dbh+0.001H-0.003Db×Dbh+0.0001Db×H-0.0002Dbh×H R^2=0.732 Res.df=1170 F=537.1 p<0.001 SEE=0.363	Wb=-0.959+0.096Db+0.144Dbh +0.0009H-0.004Db×Dbh R^2=0.340 Res.df=1172 F=152.2 p<0.001 SEE=0.597
Entada africana	Wt=0.232+0.101Db+0.141Dbh+0.002H-0.004Db×Dbh R^2=0.763 Res.df=952 F=769.2 p<0.001 SEE=0.423	Ws=-0.075+0.102Db+0.148Dbh+0.002H-0.004Db×Dbh R^2=0.737 Res.df=952 F=669.4 p<0.001 SEE=0.470	Wb=-1.352+0.069Db+0.119Dbh +0.003H-0.0001Dbh×H R^2=0.421 Res.df=952 F=174.7 p<0.001 SEE=0.695
Piliostigma thonningii	Wt=0.358+0.100Db+0.169Dbh+0.001H-0.004Db×Dbh R^2=0.693 Res.df=438 F=250.2 p<0.001 SEE=0.461	Ws=-0.083+0.105Db+0.164Dbh+0.002H-0.004Db×Dbh R^2=0.717 Res.df=438 F=281.2 p<0.001 SEE=0.465	Wb=-0.876+0.101Db+0.199Dbh-0.006Db×Dbh R^2=0.324 Res.df=439 F=71.54 p<0.001 SEE=0.763

The biomass of branches and twigs were always difficult to predict with relatively good precision compared with the stem biomass. This is in agreement with observation by Navar (2009a) that the ability to predict the biomass of large woody components

such as stems and total aboveground biomass was more accurate than that of smaller components such as branches and twigs. This suggests that within a given species, individual tree habitat (microclimate and competition with neighbors) mostly influence its upper structure; i.e., its crown geometry (as compared to stem) creating large variability at this level from tree to tree making biomass prediction difficult for this component. Poorer predictability for some species could be due to their intrinsic physical structure due to generic behavior; indeed the two *Acacia* species and *P. thonningii* usually show bushy and complicated shapes which might have made it difficult to accurately predict their biomass (especially for the *Acacia* species) from the dendrometric measures considered in this study. Competition for light between neighboring trees may also account for some of this variation; trees growing under strong competition and attaining a dominant position may produce small branches. On the other hand, trees growing in open spaces tended to have widespread crowns and large biomass in branches and twigs in contrast to that of the stem.

Several biomass equations for particular species, mixed-composition forests, specific sites, biogeographical regions, or climate-related biomes, have been published and relate tree biomass to diameter or diameter and height. Once a model has been built for a given species, it is of wide use as previous studies have revealed that no difference within species due to forest type is expected as long as the considered tree stays within the range of dendrometric measurements within which the model was developed (see for ex. Aboal et al. 2005). Moreover, published regression models are usually based on a small number of directly harvested trees and include very few large diameter trees, thus not well representing the forest at large.

It is difficult to compare the models developed in this study with other works in West Africa because of the scarcity of published results. The regressions in this study are more accurate than those of Nouvellet (1993) with the same species in a clear cut experiment in Gonsé in the Sudanian zone of Burkina Faso. Indeed, he used only the basal area parameter and the samples size was smaller. Similarly to the results in the present study, he could not find a good model for predicting biomass for *A. macrostachya*. In other savanna-woodland types such as the Zambian miombo, Stromgaard (1985) developed polynomial models using diameter at breast height, total height of the tree and fresh weight biomass and found that about 70% of the variation was explained by the models. Later Chidumayo (1990) developed a set of linear functions for mixed miombo using diameter at stump height (30 cm) and at breast height, which accounted for about 90% of the variation in wood biomass. It may be that diameter alone is a better predictor of biomass for some savanna tree species. In these studies, the sample size was rather low. In contrast, our large sample size, combined with large variation in dendrometric measurements, provides precise and useful allometric equations. Species-specific equations are very useful in assessing biomass estimates needed for accurate determination of linked factors such as carbon and nutrient storage, or for evaluation of the wood yield of species such as those in this study. The models developed in this work apply to trees of the species within the range of the structural characteristics measured. For regionally comparable estimates of biomass, an equation that incorporates terms for those aspects of forest structure that vary significantly at regional scales is required.

The current established equations may allow a rapid estimate of available biomass and thus aid in planning for sustainable use of these species. Diameter is the most common predictor in all biomass allometric models (Ter-Mikaelian and Korzukhin 1997), but adding tree height variable improves the prediction power with statistical significance. This has been noted by previous studies (Ketterings et al. 2001). This and the fact that in savanna vegetation this parameter can easily be assessed could ensure precise total biomass estimation.

Conclusion

The species-specific allometric models presented for quantifying aboveground wood biomass and biomass component in 11 woody plants in Sudanian savanna-woodland should significantly improve capacity to accurately estimate biomass, fuel loads, and carbon sequestration in the Sudanian terrestrial ecosystems. The use of dendrometric parameters from a large number of sample tree, recorded during forest monitoring as predictor variables makes the equations presented here more accurate and more likely to be used by both land managers and researchers. In addition, our models provide an ideal opportunity for further work on validation of woody biomass calculation using data on short rotation management of fuelwood. The ecological value and the value for local livelihoods of the species studied, the uniquely large sample sizes, and the breakdown of each species into morphological components make this an unusually rich data set, one that can provide insights into the biomass allocation in architecturally divergent tropical trees. However, care should be taken in extrapolating the allometric models developed in this study to other sites without knowledge of tree size structures. We recommend that the individual tree size distribution for the area of interest be evaluated and compared to the values presented in this study to determine how appropriate the allometric models are for another site.

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